

A REVISION OF *LOCHKOVELLA* CHLUPÁČ, 1972 (ARTHROPODA:  
TRILOBITA) AND A SPECIES FROM LILYDALE AND TYERS.  
PHACOPIDAE OF VICTORIA, PART 5.

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The trilobite *Acaste longisulcatus* Shergold, 1968 was described from the Early Devonian Humevale Siltstone at Lilydale, Victoria. However the holotype, an internal mould of a pygidium, is recognised as belonging to a phacopid rather than an acastid trilobite. As the original description was largely based on the paratypes, since redescribed as *A. lokii* Edgecombe, 1993, the holotype and its species have been poorly understood. The species is assigned here to *Lochkovella* Chlupáč, 1972, not previously recorded in Australia but well represented by *L. longisulcata* and three other species from Victoria and New South Wales. The relationships of *Lochkovella* are reviewed, and a revised generic diagnosis is provided. *Lochkovella longisulcata* is abundant in the middle horizons of the Humevale Siltstone at Lilydale and in the upper horizons of the Boola Formation at Coopers Creek and Tyers. The stratigraphic ranges of *L. longisulcata* and 15 other trilobite and brachiopod taxa common to the Tyers and Lilydale sequences suggest correlation of the fauna from the upper horizons of the Boola Formation with faunas from the 1 700 m – 2 400 m interval of the Humevale Siltstone at Lilydale. Age estimates on these sequences are not well constrained and range within the early Lochkovian to earliest Pragian interval, accommodating divergent interpretations of the upper boundary of the Boola Formation with the overlying Coopers Creek Limestone.

*Keywords:* Trilobites, Phacopidae, Systematics, Victoria, Devonian

TRILOBITES occur in abundance in the marine fauna of the Late Silurian-Early Devonian Humevale Siltstone (3 800 m thick) at Lilydale, 35 km E of Melbourne (Fig. 1). Twenty-nine trilobite species, mostly undescribed, are represented by 750 specimens from about 50 different localities between Christmas Hills (35 km ENE of Melbourne) and Lilydale, ranging variously throughout the unit (Fig. 2). A poorly documented phacopid, assigned below to *Lochkovella* Chlupáč, 1972, occurs at localities at horizons between 465m and 2 400 m above the base of the unit. Occurrences of the species include locality PL1820 (G20 'Ruddocks Quarry'), Chirnside Park (600 m horizon) and locality PL1804 (G4, 'Flowerfield Quarry'), Coldstream (1755 m horizon). Specimens from the latter locality were figured by McCoy (1876) as '*Phacops (Portlockia) fecundus* Barrande, 1846'. The former locality is the type locality for several trilobite species including '*Goldins greenii* Chapman, 1915, *Sthenarocalymene angustior* (Chapman, 1915), *Acastella frontosa* Shergold, 1968 and the problematic *Acaste longisulcatus* Shergold, 1968. The latter species is not an acastid; Holloway & Neil (1982) noted that the pygidium figured by Chapman (1915) as '*Phacops*

*crossicci* Etheridge & Mitchell, 1896' and later designated holotype of *A. longisulcatus* is a phacopid. The paratypes of *A. longisulcatus* (from PL1850 [G50, 'Black Springs Quarry'], Chirnside Park) are not conspecific with the holotype; they belong to an acastid trilobite and were described as *Acaste lokii* Edgecombe, 1993. As the specimens of *Lochkovella* from PL1820, from PL1804 (including some of McCoy's figured specimens) and other localities are conspecific with the holotype of *longisulcatus*, they permit the redescription of *L. longisulcatus*.

Philip (1962) described a trilobite fauna from the Boola Formation at Tyers, about 130 km ESE of Melbourne, including *Cheirurus (Cheirurus)* sp. occurring at the stratigraphically lowest trilobite locality, with *C. (Crotalocephalus) silverdalensis* Etheridge & Mitchell, 1917, *S. angustior* and *Leonasps bispinosa* Philip, 1962 occurring in the upper horizons of the unit. Philip did not record any phacopid trilobites in the Tyers fauna, but in his and other fossil collections from the area two species are represented, *Boeckops* sp. and *Lochkovella longisulcata*, the latter also occurring in the unit at Coopers Creek, about 20 km NNE of Tyers. Other trilobites occurring in the Boola Formation at

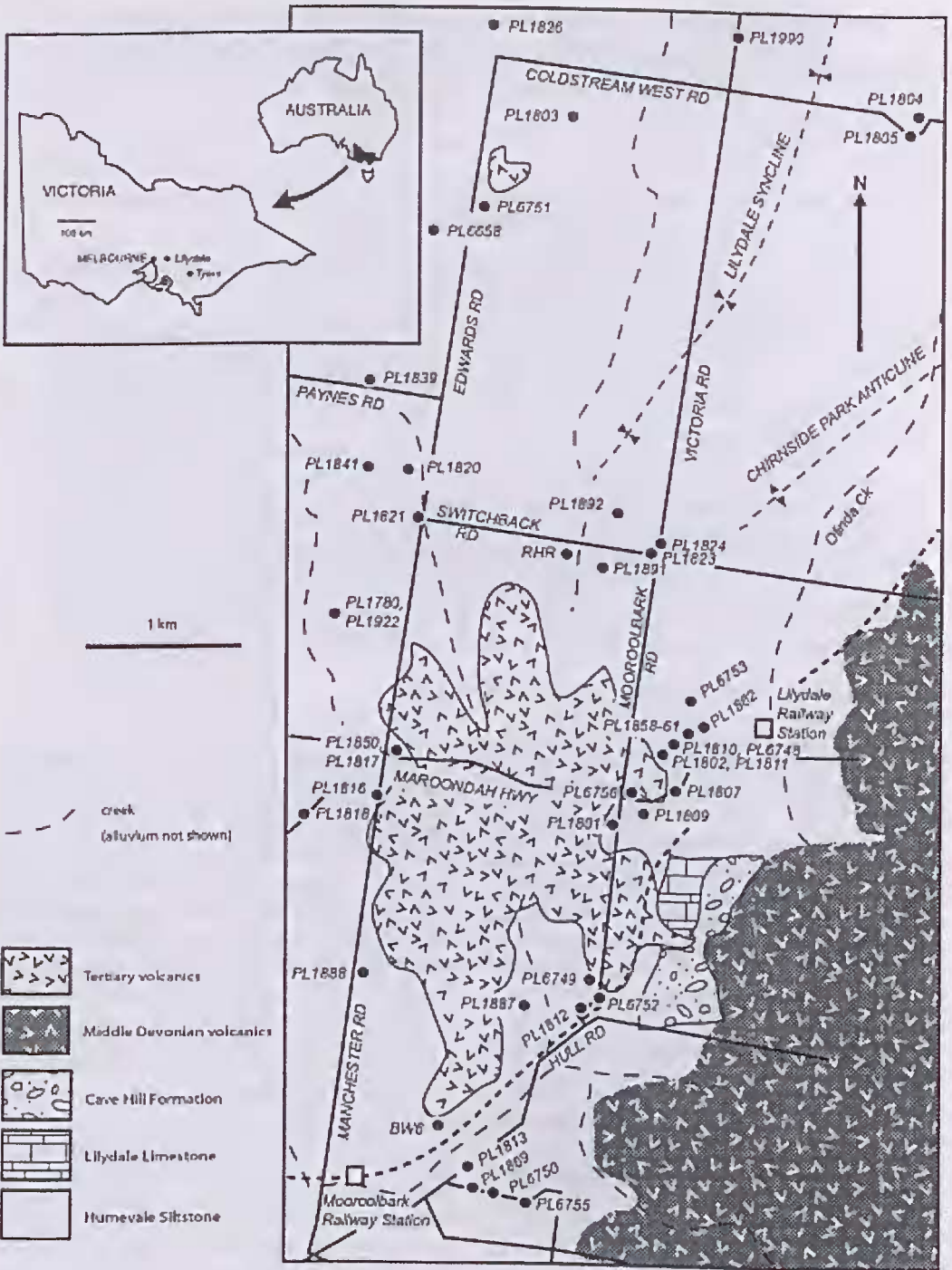


Fig. 1. Fossil localities in the Lilydale area. Geology follows Vandenberg (1970), Garratt (1972) and Wall et al. (1995). AMG gridlines and coordinates shown.

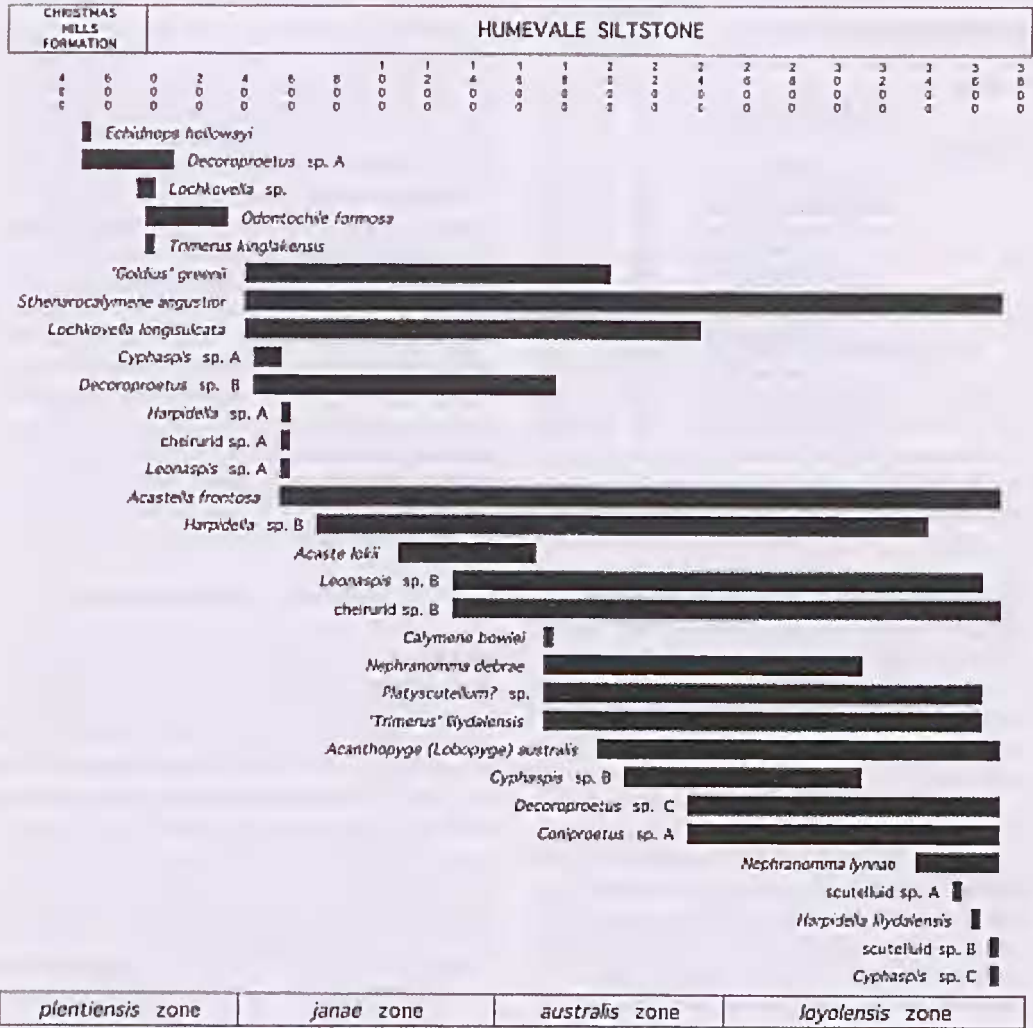


Fig. 2. Stratigraphic distribution of trilobites from the Christmas Hills-Lilydale sequence, in order of first appearances.

Coopers Creek include *S. angustior*, '*Goldius*' *cresswelli* Chapman, 1915, *Dicranurus* sp. and indeterminate proctid, aulacopleurid and lichid species.

BIOSTRATIGRAPHY, CORRELATION AND AGE

The trilobite fauna of the Humevale Siltstone occurs with an abundant brachiopod fauna, represented by at least 75 species (Garratt 1983; Fig. 5) and spanning four of the brachiopod assemblages described by

Garratt (1983) and Garratt & Wright (1988) including the *Notoparmella plentiensis* Assemblage Zone (ranging up to the 400 m horizon), the *Boucotia janae* Assemblage Zone (ranging from the 400 m to the 1 500 m horizon), the *Boucotia australis* Assemblage Zone (ranging from the 1 500 m to the 2 500 m horizon) and the *Boucotia loyolensis* Assemblage Zone (ranging up from the 2 500 m horizon). Deriving age constraints from various brachiopod taxa and from graptolite, dactyloconarid and conodont faunas from other areas, Garratt & Wright correlated the base of the *janae* zone with the Siluro-Devonian boundary, and correlated the *australis* zone with the late Lochkovian *Monograptus*



Brachiopod and trilobite taxa represented in the upper Boola Siltstone at Tyers		Stratigraphic range at Lilydale (measured above base of Humevale Siltstone)	
<b>TRILOBITES</b>			
	<i>Lochkovella longisulcata</i>	465	to 2400
	<i>Sphenaroclymene angustior</i>	465	to 3800
<b>BRACHIOPODS</b>			
	<i>Lissatrypa lenticulata</i>	50	to 3720
	<i>Plectodonia bipartita</i>	300	to 3620
	<i>Cymostrophia euglyphoides</i>	465	to 3720
	<i>Strophonella gypsilandica</i>	465	to 2600
	<i>Eospinifer eastoni</i>	500	to 3720
	<i>Spinatrypa limbriata</i>	540	to 3620
	<i>Notoleptaena ctophara</i>	560	to 3720
	<i>Maonstrophia kabiei</i>	600	to 3620
	<i>Boucotia australis</i>	1120	to 3620
	<i>Strophochonetes' cresswelli</i>	1520	to 3720
	<i>Notonopsis philipi</i>	1650	to 2960
	<i>Hysterolites Mydalensis</i>	1700	to 3620
	<i>Schizophoria</i> sp. nov. A.	1700	to 3720
	<i>Leptostrophia affinitata</i>	2520	to 3720

Fig. 3. List of trilobite and brachiopod taxa common to the Tyers and Lilydale sequences, and their stratigraphic ranges at Lilydale.

*hercynicus* graptolite Biozone. They correlated the base of the *loyolensis* zone with the Lochkovian-Pragian boundary; although elsewhere Garratt (1983: 86) assigned the lower horizons of the *loyolensis* zone at Lilydale to the late Lochkovian. From these age estimates, *L. longisulcata* ranges through the early and late Lochkovian, but excluding the earliest and latest Lochkovian.

The lithology and fauna of the Boola Formation were described in detail by Philip (1962). Problems regarding the nomenclature and correlation of strata currently referred to the Boola Formation and the overlying Coopers Creek Limestone were discussed by Mawson & Talent (1994). The age of the fauna occurring high in the Boola Formation is poorly constrained, with successive revisions providing younger age estimates. Philip (1960) considered that elements of the brachiopod fauna from the upper 45 m of the unit indicated a Ludlow age but, following the revision of indicator taxa in Belgium (Boucot 1960), Philip (1962) dated the assemblage as early Lochkovian. Savage (1973) correlated the fauna with the early Lochkovian *Gypichila pelagica* brachiopod Biozone. Garratt (1983) assigned the fauna to the *australis* zone, inferring a late Lochkovian age, although he noted the presence of *Lissatrypa lenticulata*, considered an index species of the *loyolensis* zone elsewhere. Mawson & Talent (1994) suggested that the *australis* zone ranged into the lower parts of the *sulcata* zone (earliest Pragian). A minimum age of the Boola Formation fauna is constrained by conodont assemblages from the base of the overlying Coopers Creek Limestone, correlated by Mawson & Talent with the upper part of the

*Eognathodus sulcata* conodont Biozone (early Pragian).

In considering the ranges of the 16 brachiopod and trilobite species that co-occur in the Lilydale fauna and the Tyers fauna, the strongest similarity of the Tyers fauna is with the faunal succession ranging in the 1 700 m – 2 400 m and 2 580 m – 2 600 m intervals of the Humevale Siltstone at Lilydale, in which 15 of the 16 species common to both sequences are represented (Fig. 3). Emphasis on the last appearance of *Lochkovella longisulcata* suggests correlation with the lower interval. Unfortunately, this broad biostratigraphic correlation of the faunas is of limited significance in the age estimate of the Tyers fauna, as the age of the Humevale Siltstone fauna also remains poorly constrained. Despite the recently revised generic assignments of taxa represented at Lilydale (Talent et al. 2001), limited reliance can be placed on age constraints derived from the stratigraphic ranges of individual brachiopod and trilobite genera. Specifically, several genera considered by Brice *et al.* (2000) and Chlupáč *et al.* (2000) to be significant in the recognition of stage boundaries occur at Lilydale, but are anomalous with respect to their documented ranges. There is a greater degree of accord in the age suggested by trilobite species considered closest to those at Lilydale. The trilobite *Trimerus lilydalensis* Gill, 1949 (appearing at the 1 755 m horizon) belongs to a species group ranging no lower than the late Lochkovian elsewhere, and most closely resembles the poorly known late Lochkovian *Digonus' bostoviensis* Tomezykova, 1975 from Poland. *Lochkovella longisulcata* (last appearance at the 2 400 m horizon) most closely resembles the type species *L. misera* (Barrande, 1852) from the late Lochkovian-basal Pragian of Europe. Shergold (1968) compared his new species *Acastella frontosa* (ranging 550 m – 3 700 m interval) with *A. patula* Hollard, 1963 from the early Lochkovian of Morocco, and compared specimens of *Acaste lokii* Edgecombe, 1993 (ranging 1 100 m – 1 700 m interval) with *A. dayiana* Richter & Richter, 1954 from the early Lochkovian of Germany. These comparisons support a late Lochkovian age for the 1 700 m–2 400 m interval of the Humevale Siltstone.

There has been ongoing debate on the nature of the boundary between the Boola Formation and the overlying Coopers Creek Limestone. Philip (1965, 1968) argued that sedimentary features at the base of the Coopers Creek Limestone indicated a significant hiatus with respect to the Boola Formation. However, Mawson & Talent (1994) reinterpreted these features as localised and cited other features to support the overall conformity of the units. Poor constraints on the age

of the Boola Formation accommodate these divergent interpretations of the nature of its upper boundary with the Coopers Creek Limestone at Tyers. The early Loehkovian and late Loehkovian age estimates suggest a earliest Pragian hiatus to underlying the base of the Coopers Creek Formation, whereas earliest Pragian age estimates support interpretation of the sequence as conformable. Perhaps the most compelling support for a late Loehkovian rather than early Pragian age for the Tyers fauna is provided not by faunal elements, but by close alignment of the suggested hiatus between the Boola Formation and the Coopers Creek Limestone with the 'pre-1A' eustatic regressive phase recognised across North America by Johnson & Sandberg (1988). This event is correlated with the *pesavis* zone-early *snleatns* zone (latest Loehkovian-earliest Pragian) interval, and is documented elsewhere as the basal Pragian boundary event (Walliser *in* Weddige 1998; Chlupáč & Kukul 1986).

#### SYSTEMATIC PALAEOLOGY

Trilobite specimens described here are preserved as internal and external moulds. For photography, internal moulds have been coated with colloidal graphite, external moulds have been prepared as latex peels, and all were whitened with ammonium chloride. Specimens housed in the Melbourne Museum are registered with the prefix NMV P. Trilobite localities cited in the text include localities registered at the Melbourne Museum (prefixed PL), Geological Survey of Victoria localities (prefixed GSV), G. Sweet localities (prefixed Y or YF) and E. D. Gill localities (prefixed G). These and other localities are mapped in Gill (1940, 1945), VandenBerg (1970), Garratt (1977) and Wall *et al.* (1995).

Order Phacopida Salter, 1864

Suborder Phaeopina Richter, Richter & Struve, 1959

Superfamily Phaeopoidea Hawle & Corda, 1847

Family Phacopidae Hawle & Corda, 1847

Subfamily Phaeopinae Hawle & Corda, 1847

Genus *Lochkovella* Chlupáč, 1972

*Type species.* *Phacops miser* Barrande, 1852 from the Loehkov Formation (Loehkovian, *hercyniens* Zone, Early Devonian), Loehkov, Czech Republic.

*Species assigned.* *Reedops deckeri* Delo, 1935;

*Ananaspis ekphymus* Jones, Hall, Wright & Carr, 1986; *Phacops fecundus minor* von Gaertner, 1930; *Phacops grimbergi* Frech, 1888; *Phacops (Phacops?) hannsi* Chlupáč, 1977; *Phacops heritschi* von Gaertner, 1930; *Acaste longisulcatus* Shergold, 1968; *Phacops (Phacops?) veles* Chlupáč, 1972; *Kainops* sp. cf. *ekphymus* (*in* Ebach 2002); *Reedops* sp. nov. (*in* Holloway *in* Jell & Holloway 1983).

*Range.* Ludlow-Pragian.

*Revised diagnosis.* Glabella moderately convex, with front of glabella overhanging anterior border in dorsal view. Preoccipital ring as high as glabella anterior to L1. S2-S3 shallow to moderately deep. Eye placed with anterior margin adjacent to lateral border furrow. Glabellar ornament variable, ranging between moderately-sized tubercles to coarse granulation. Coarse to fine granulation on entire exoskeleton. Vincular furrow of variable depth, lateral notching indistinct. Hypostome inflated with middle furrow poorly defined, posterior border of moderate length. Pygidium with 6-7 deep pleural furrows that are uniform in depth to border, posterior furrows not markedly shallowed; interpleural furrows a well-defined incision, reaching border.

*Discussion.* Chlupáč (1972) erected *Lochkovella* to accommodate species previously assigned to *Denckmannites*, restricting the latter to the type, *D. volborthi* (Barrande, 1852). Campbell (1977) regarded *Lochkovella* as a subgenus of *Denckmannites*, noting that both taxa share relatively narrow axial and wide pleural proportions that distinguish them from most other phacopids. Chlupáč (1977) noted the rich segmentation of the pygidia shared by the two genera, and suggested possible derivation of *Lochkovella* from *Denckmannites*. This view was shared by Campbell, who considered the main difference between the groups to be the continuous anterior cephalic border of the latter. Chlupáč (1977) listed further differences, including the greater convexity and forward projection of the glabella of *Lochkovella*, as well as its shorter hypostome and more distinct interpleural furrows. The differences between *Lochkovella* and *Denckmannites* are considered here to be profound and to support the full generic status of *Lochkovella*. *Denckmannites* is characterised by an unusually narrow glabella and an extraordinarily narrow pygidial axis (far narrower than those of *Lochkovella*), and large L1. Rich pygidial segmentation in the genera is manifestly different, in *Denckmannites* being expressed by a high number of pleural furrows (8 to 9) but in *Lochkovella* by well-



defined interpleural furrows (5 to 7). In addition, though the length of the eye is short in both *Lochkovella* and *Denckmannites*, the visual surface is differently developed, being highly reduced in *D. volborthi* but normally developed in *Lochkovella*. The similarities between these genera have been overstated and do not signify a close relationship. Rather, the specialised morphology of *Denckmannites* is analogous to that of other deep-water phacopids and reflects no more than adaption to the environment. Morphoclines involving eye length, pygidial segmentation and glabellar development recognised by Chlupáč between *Denckmannites*, *Lochkovella* and *Reedops* are based on very generalised characters and do not indicate ancestor-descendant relationships as suggested by Campbell and Chlupáč.

The concept of *Lochkovella* described in the revised diagnosis here is much wider than that of Chlupáč (1977), and embraces a number of species previously assigned to *Reedops*, *Ananaspis*, *Phacops* and *Kainops*. *Lochkovella* differs from *Reedops* in having strongly expressed cephalic ornament that often extends over the entire exoskeleton, distinct S2-S3, and a lower cephalic length/width ratio (0.59 in *L. misera*; cf. 0.65-0.72 in *Reedops*). Chlupáč described the glabella of *Lochkovella* as overhanging the anterior border, as in *Reedops*, although in glabellar profile the latter can be distinguished by its stronger inflation and, in some species, its more forward projection. In pygidial features *Lochkovella* can be easily distinguished from *Reedops* by the more robust appearance of the latter, being proportionally narrower and with a wider and more inflated axis, and with pleural furrows shallowing abruptly posteriorly with very weak to effaced interpleural furrows. Species previously assigned to *Reedops* include the Lochkovian *R. deckeri* Delo, 1935 from Oklahoma. Ormiston (1968) excluded *deckeri* from *Reedops* on the basis of its medially distinct vincular furrow. The depth of S2 and S3, the extensive granulate ornament and the depth and uniformity of pygidial pleural and interpleural furrows are also considered here as significant in distinguishing the species from that genus and in supporting assignment to *Lochkovella*. Similar features indicate that the closely comparable *Reedops* sp. nov. of Holloway in Jell & Holloway (1983) belongs to *Lochkovella*. The species occurs stratigraphically below *L. longisulcata* in the lowermost 100 m of the Humevale Formation at Christmas Hills. Associated faunal elements correlate with the *plentiensis* zone, considered here to span the late Ludlow-Pridoli. The species is distinguished in having a glabellar ornament of finer granules that extend, with little change in size or density, over the entire

exoskeleton.

Although Campbell (1977) and Chlupáč (1977) also suggested possible derivation of *Lochkovella* from *Ananaspis*, recognising strong resemblances in pygidial morphology, there has been very little other consideration given to the relationship between *Ananaspis* and *Lochkovella*. Chlupáč did not explicitly compare *Lochkovella* with *Ananaspis*, and Campbell noted only that the glabellar shape of *Lochkovella* is more similar to *Ananaspis* than to *Reedops*. Ramsköld & Werdelin (1991) made no reference to *Lochkovella* in their cladistic analysis of Silurian-Early Devonian phacopids. In overall cephalic and pygidial morphology *Lochkovella* and *Ananaspis* are very similar, and the separation of the genera is not straightforward. Characters considered of significance in distinguishing *Ananaspis* include the presence of vincular notching (indistinct in *Lochkovella*), more proximally and higher-placed eyes (antero-laterally placed eyes in *Lochkovella*), a librigenal field separating the eye from the lateral border furrow (absent in *Lochkovella*) and more deeply incised interpleural furrows (shallower in *Lochkovella*). Emphasis on the lateral notching of the vincular furrow and the proximal placement of the eyes is justified by their conservative expression in presumably descendant groups of *Ananaspis* including *Paciphacops* and *Echidnops*. Morphology of the hypostome is another way of distinguishing the genera, although information is available for few species; the hypostome of *L. misera* exhibits a long posterior border, whereas in *A. fecundus* (and *Echidnops* and *Paciphacops*) it exhibits a short posterior border.

Species previously assigned to *Ananaspis* include the Lochkovian *A. ekphymus* Jones, Hall, Wright & Carr, 1986 from Bungonia, New South Wales. Ramsköld & Werdelin (1991) considered *A. ekphymus* to be conspecific with *Paciphacops* (*Paciphacops*) *microps* Chatterton, Johnson & Campbell, 1979 from the Pragian of Wellington, New South Wales, nominated as the type species of their new genus *Kainops*. However, *ekphymus* can be distinguished in having much denser and more uniformly sized cephalic and post-cephalic tuberculation, a vincular furrow that is almost indistinct medially, and a shorter eye and longer postocular genae (postocular length/eye length 0.6 in *ekphymus*; cf. 0.5 in *microps*). These differences are in accord with its assignment to *Lochkovella*. Following Ebach (2002), *ekphymus* is maintained here as an independent species. Ebach documented a species close to *ekphymus* from the Lochkovian-?Pragian at Cobar, New South Wales. The species differs from *ekphymus* in having much smaller cephalic tubercles and an even longer postocular genal length (eye length/postocular

genal length 0.7-1.0).

Species previously assigned to *Phacops* include two Pragian Czech species described by Chlupáč (1977) as *Phacops* (*Phacops*?) *hauusi* and *P.* (*P?*) *veles*. Chlupáč considered that these species represent morphologies intermediate between *Ananaspis* and *Phacops* and show some similarities to *Reedops*, and they were more recently placed in *Kainops* by Ramskold & Werdelin (1991). The finely tuberculate ornament of the exoskeleton, the well-defined pygidial segmentation and the antero-lateral placement of the eye indicate assignment to *Lochkovella*. In the low contrast between cephalic and post-cephalic ornament, these species are closest to *L. deckeri* and the species from Cobar and Christmas Hills.

Species previously assigned to *Lochkovella* by Chlupáč (1977) but excluded here include two species figured by Alberti (1970), *Phacops* (*Reedops*) sp. A aff. *akonchensis* (G. & H. Termier, 1950) and *Phacops* (*Reedops*) sp. B aff. *akonchensis*, both from Morocco. With further material Alberti (1983) redescribed these as species of *Phacops* (*Prakops*). *Denckmannites rutherfordi* Sherwin, 1968 from the Late Silurian Wallace Shale of New South Wales is also excluded from *Lochkovella*, differing from assigned species in having strongly defined notches on the vineular furrow.

*Lochkovella longisulcata* (Shergold, 1968)

Fig. 4A-S, Fig. 5A-S

1876 *Phacops* (*Portlockia*) *fecundus* (Barrande); McCoy, p. 15-16, pl. 22, figs 8-9; pl. 23, figs 2-3, non pl. 23, figs 1, 4-6 (= *Nephranomma*

*debrac* Sandford, 2003).

- 1896 *Phacops sweeti* Etheridge & Mitchell, p. 497 (non figs = *Nephranomma sweeti* Etheridge & Mitchell, 1896).
- 1915 *Phacops crossleii*; Chapman, p. 168, pl. 15, fig. 15 non fig. 14 (= *Acaste lokii* Edgecombe, 1993)
- 1938 *Phacops fecundus*; Gill, p. 170 (pars).
- 1940 *Phacops fecundus* McCoy non Barrande; Gill, p. 250 (pars).
- 1951 *Phacops* sp. nov.; Gill, p. 31 (pars).
- 1968 *Acaste longisulcata* Shergold; p. 20, pl. 4, figs 7-8 non pl. 5, figs 1-12 (= *Acaste lokii* Edgecombe, 1993).
- 1996 *Ananaspis* sp. 1; Sandford, p. 220, pl. 26, figs A-II, non fig. 1 (= *Ananaspis* sp.)

*Type material.* Holotype P12680 (pygidium, figured Chapman 1915: pl. 15, fig. 15, figured Shergold 1968: pl. 4, figs 7-8) from PL1820 (G20, 'Ruddocks Quarry'), Chirnside Park. The paratypes of *Acaste longisulcata* including P25230-38, P25240 (all from PL1850 (G50, 'Black Springs Quarry'), Chirnside Park form the type series of *Acaste lokii* Edgecombe, 1993.

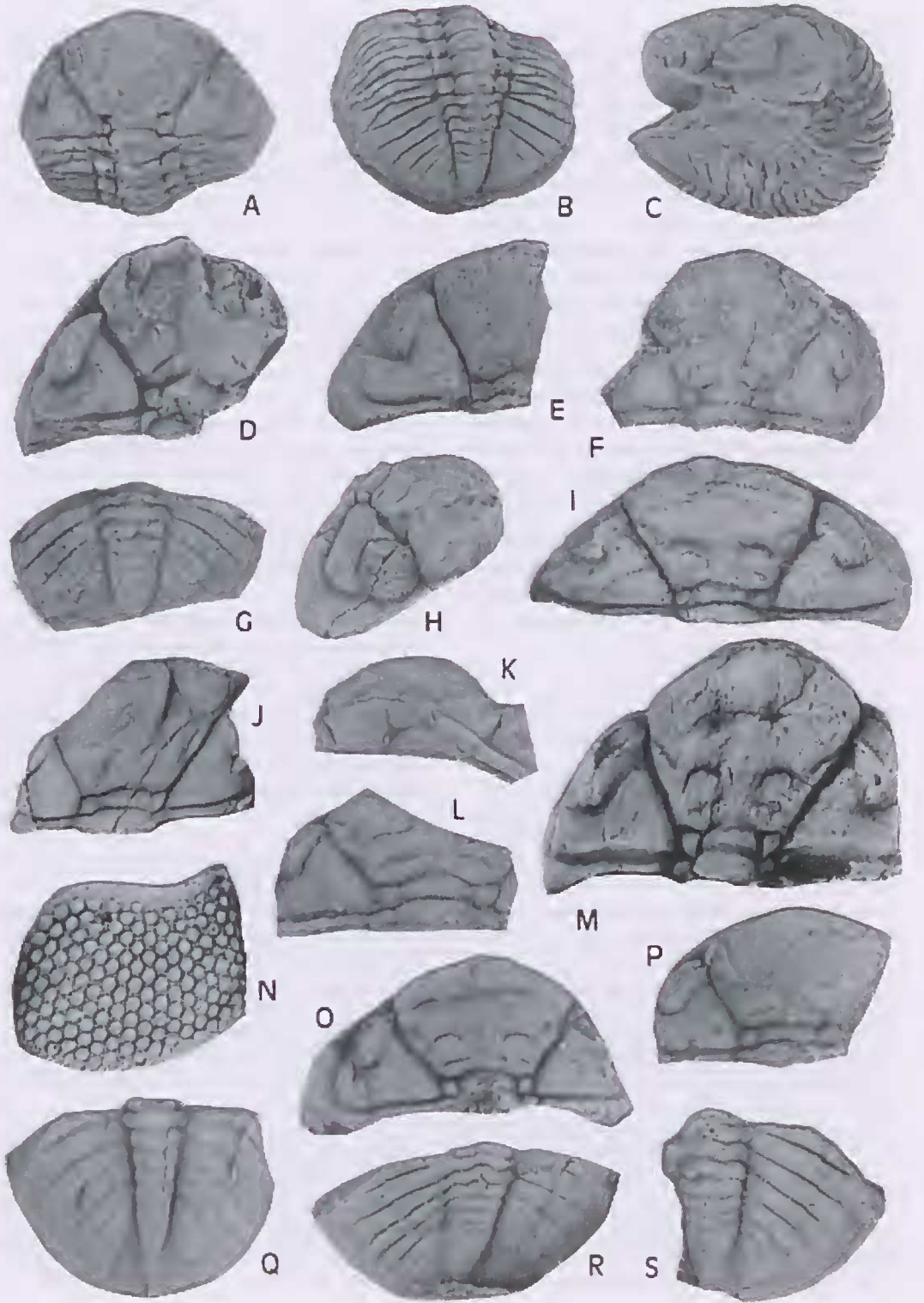
*Figured specimens.* P12118 (enrolled exoskeleton, figured McCoy 1876: pl. 23, figs 2, 3) from PL1804 (GSV B15, 'Section 12, Parish of Yering') Coldstream, considered by Gill (1940) the same locality as G4, 'Flowerfield (or Mic Blacks) Quarry'. The cephalon and the pygidium figured by McCoy (1876: pl. 22, fig. 8, fig. 9 respectively) are missing but, from his illustrations they can also be confidently attributed to *L. longisulcata*.

*Other material.* 100 specimens: four exoskeletons, 39

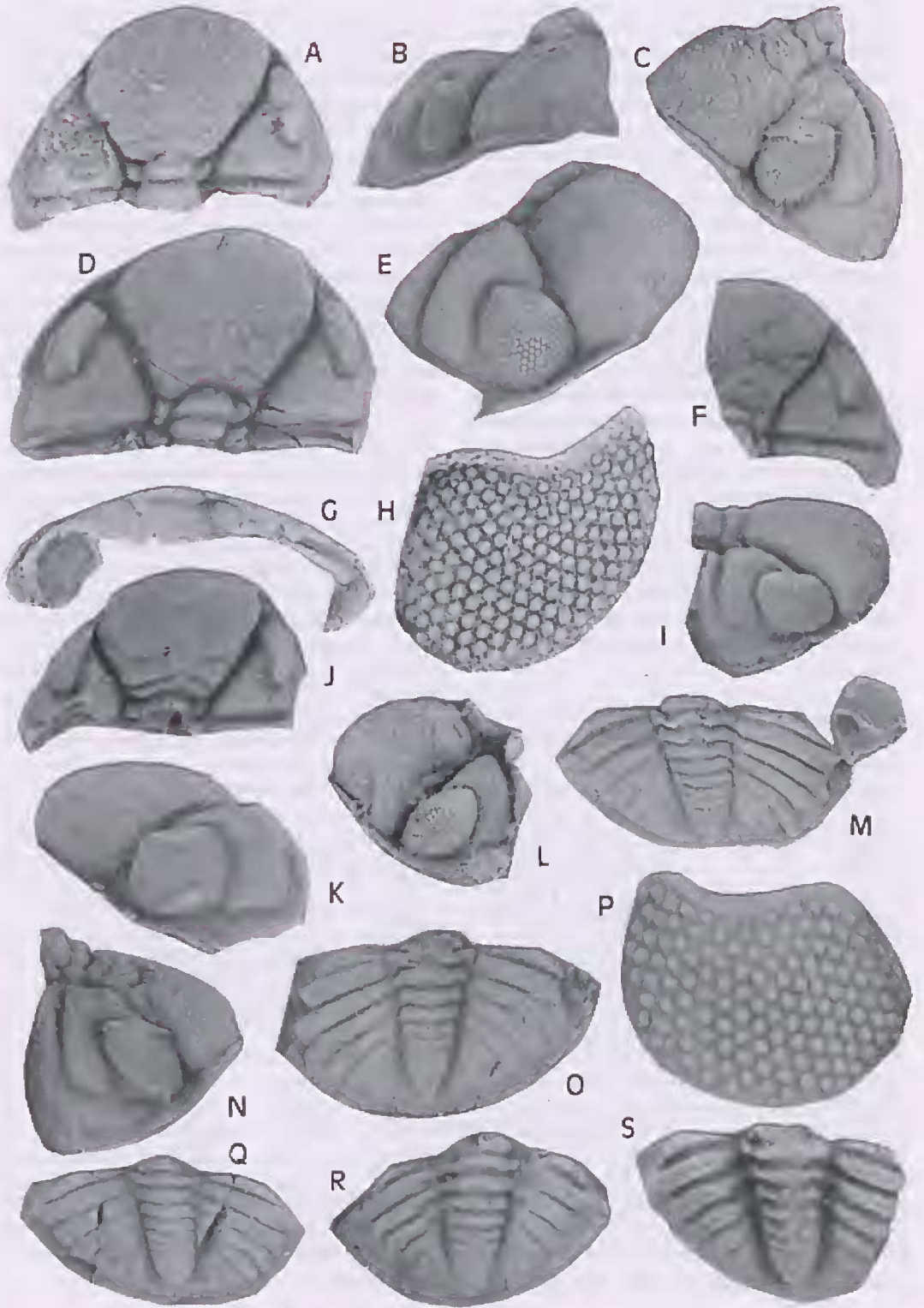
Fig. 4. *Lochkovella longisulcata* (Shergold, 1968). A-C. P79123, enrolled exoskeleton, internal mould, A, dorsal view of cephalon x 1.0. B, lateral view x 1.25. C, dorsal view of pygidium x 1.0. D. Topotype P306868, cephalon, internal mould, dorsal view x 2.8. E. P12117, cephalon, internal mould, dorsal view x 1.6. F. P12118, cephalon, latex cast, dorsal view x 1.4. G. P306751, pygidium, internal mould, dorsal view x 1.8. H. P308933, cephalon, internal mould, oblique view x 1.75. I. P306919, cephalon, internal mould, dorsal view x 1.8. J. P308920, cephalon, latex cast, dorsal view x 3.0. K. P308925, cephalon, internal mould, ventral view (doubleure) x 2.0. L. P306750, cephalon, latex cast, dorsal view x 2.3. M. P137147, cephalon, internal mould, dorsal view x 2.5. N. P308931, cephalon, latex cast, enlargement of eye x 9.0. O. P308919, cephalon, internal mould, dorsal view x 1.8. P. P308924, cephalon, internal mould, dorsal view x 2.2. Q. P308926, pygidium, latex cast, dorsal view x 2.4. R. P308928, pygidium, latex cast, dorsal view x 2.5. S. P308930, pygidium, latex cast, dorsal view x 2.5. A-G, I, M from the Humevale Siltstone. H, J-L, N, S from the Boola Formation.

Fig. 5. *Lochkovella longisulcata* (Shergold, 1968). A, I. P306914, cephalon, internal mould x 4.5. A, dorsal view. I, lateral view. B, C, F, H, N. P306875, cephalon. B, internal mould, anterior view x 2.75. C, latex cast, oblique view x 2.75. F, internal mould, dorsal view x 2.25. H, latex cast, enlargement of eye x 9.0. N, latex cast, lateral view x 2.75. D, E, M, P. Topotype P306864, partly enrolled exoskeleton. D, internal mould, dorsal view of cephalon and first thoracic segment x 3.3. E, latex cast, oblique view of cephalon x 4.0. M, internal mould, lateral view of cephalon x 4.4. P, latex cast, enlargement of eye x 12. G. Topotype P306867, cephalon, latex cast, ventral view (doubleure) x 3.0. J. P306876, cephalon, internal mould, dorsal view x 3.7. K, L. P306872, cephalon. K, latex cast, oblique view x 5.0. L, external mould adjacent to large pygidium x 2.0. M. P306871, pygidium, internal mould, dorsal view x 2.0. O. P306916, pygidium, internal mould, dorsal view x 2.4. Q. Topotype P306865, pygidium, internal mould, dorsal view x 2.0. R. Holotype P12680, pygidium, internal mould, dorsal view x 2.5. S. P306877, pygidium, internal mould, dorsal view x 3.0. Humevale Siltstone.









cephala, one partly disarticulated thoracopygon, 56 pygidia. *Chirnside Park-Coldstream area*: Topotypes P306864-70 from PL1820, P137147-9, P140153 probably from PL1820. Unregistered specimen from PL1839 (G39, 'North of Ruddocks'), Chirnside Park. P306890-1 from PL1817 (G17, 'Black Springs Cutting'), Chirnside Park. P306916-17 from locality RHHR (corner of Brentwoods and Rolling Hills Road), Chirnside Park. P26089 from PL1891 (G91), Chirnside Park. P79214, P306871-2, P306875-85, P306887-89 from PL6751, Chirnside Park. P306914-15 from PL1892 (G92), Chirnside Park. P306753-7, P306764 from PL1804 (YF, 'Yarra Flats'). P306758 from PL1804 (Y, 'Yering'). P12117, P306750-1, P306759 from PL1804 (GSV B15). P79123 from PL1804 or PL1805 (G5, 'Flowerfield Cutting'), Coldstream. *Mooroolbark area*: P306919-20, P306986 from locality BW6 (corner of Winyard Drive and Baradine Road), Mooroolbark. *Tyers area*: P308919, P308953-4 from PL337, Tyers. P308920-8, P308939-50 from PL334, Tyers. P308929 (ex GSV 19377), P308952 from 'Tyers River' (exact locality unknown). P308930-1 from 'Tyers' (exact locality unknown). P308955 from 'near Tyers Quarry' (exact locality unknown). *Coopers Creek area*: P308956 from PL1797, Coopers Creek. P308933-4 from 'Coopers Creek' (exact locality unknown). P308951 from Evans Brothers Quarry, Coopers Creek.

*Revised diagnosis.* *Lochkovella* with anterior margin of glabella broadly rounded, with arc of curvature cen-

tred at about 0.25 cephalic length. Axial furrows weakly sinusoidal. Eye large for genus, length (exsag.) 0.37 times cephalic length, with midline placed opposite 0.53 cephalic length. Visual surface with 17-25 (mostly 18-21) lens files of up to 7-10 lenses per file and between 105-180 lenses. Postocular genal length (exsag.) 0.25 times cephalic length and 0.7 times length of eye (ranging to 0.2 times cephalic length and 0.4 times eye length in smaller specimens). Glabellar tuberculation comprising small, sparsely to densely distributed tubereles interspersed with dense ornament of granules, granulation coarser anteriorly, tubereles larger posteriorly. Palpebral area and postocular genae with subduced tuberculation. Vincular furrow indistinct medially, without notehing laterally. Pygidium with 7-9 axial rings, 6-7 pleural ribs. Cephalic doublure and pygidium with ornament of fine granulation.

*Description.* Estimated maximum length 9 cm (based on specimen P79123). Cephalon roughly semicircular in dorsal outline, length about 0.56 times width. In anterior view glabella moderately convex, in lateral view, dorsal outline weakly convex posteriorly, strongly convex anteriorly, with anterior surface of glabella vertical. Glabellar length about equal to maximum width, anterior to occipital furrow expanding strongly forwards with maximum width about 0.6 times cephalic width and about 1.75 times occipital width, maximum glabellar width placed opposite 0.75 cephalic length. Occipital ring width 0.35 times cephalic width, length (sag.) 0.13 times cephalic length, with deep longitudi-

SPECIMEN	CEPHALIC LENGTH	LENS FORMULA	TOTAL LENSES	TOTAL FILES
P306872	5.5 mm	5 6 7 7 7 8 7 7 6 7 7 6 7 6 5 6 6 5 4 3 2	124 lenses	21 files
P306914	7 mm	. . 8 8 7 8 7 8 9 9 9 8 8 8 7 7 6 5 4 2	~140 lenses	20 files
P306876	7.5 mm	6 7 9 # # # # # . . . . .		21 files
P306867	9 mm	5 7 7 7 7 7 7 7 7 . . . . 6 6 4 3	~115 lenses	18 files
P306864	10 mm	5 7 7 8 8 8 8 8 8 8 8 8 7 7 6 5 4 1 right eye	129 lenses	19 files
		. . 8 8 8 9 9 8 8 8 8 6 6 6 7 6 5 4 2 left eye	~129 lenses	19 files
P306891	10 mm	4 6 6 6 7 7 7 8 8 8 7 7 6 6 5 5 2	105 lenses	17 files
P306868	11 mm	4 5 7 7 7 7 7 8 8 8 7 7 6 7 6 6 5 4	116 lenses	18 files
P306875	12 mm	5 7 8 9 9 # # # 9 9 9 8 9 9 9 8 7 7 5 5 3	165 lenses	21 files
P306919	13 mm	4 6 8 8 8 9 . . . . . 8 7 6 5 6 5 3 2	~135 lenses	20 files
P137149	13 mm	. . . . . 9 9 8 9 9 8 8 8 7 6 5 3 1		25 files
P308931		3 7 8 9 # 9 # 9 # 9 9 8 8 7 8 8 7 8 8 4 3 1	172 lenses	23 files
P306754	14 mm	6 7 7 8 9 9 # # # # 9 . . . . .	~160 lenses	20 files
P306869	~15 mm	5 7 8 8 9 8 9 8 9 8 8 7 7 7 6 5 5 3	127 lenses	18 files
P137147	~15 mm	6 7 8 9 # # 9 # # 8 9 8 9 9 ? ? ? ? ? 7 6 5	~180 lenses	22 files
P306752	17 mm	. . . . . 8 9 8 9 8 8 7 8 8 . . . . 4 2		20? files

Table 1. Visual surfaces of specimens of *Lochkovella longisulcata* (Shergold, 1968).



nal furrow impressed into anterior margin of occipital ring opposite L1 and continuing across occipital ring as moderately impressed furrow, defining lateral occipital lobes, length (exsag.) of lobes about 0.5 times sagittal length of occipital ring. Medial section of occipital furrow transverse, and moderately impressed, short (sag.) on external surface, longer on internal moulds, lateral section offset (posteriorly), directed antero-laterally (at about 20° to the transverse) and deep. Medial section of pre-occipital ring with length about 0.07 times cephalic length, length 0.25 times width, in lateral view at same height as glabella anterior to L1. L1 isolated from preoccipital ring by longitudinal furrow, deep at anterior margin of ring and moderately impressed posteriorly. L1 quadrate, flat, length of L1 (exsag.) 0.1 cephalic length. L1-L1 0.9 times occipital width. S1 deep and transverse, continuous with preoccipital furrow that is shallow and long (sag.).

Eye oriented at about 20° to the sagittal line. Visual surface with highly variable lens count, with 17-25 (mostly 18-21) lens files of up to 7-10 lenses per file and between 105-180 lenses in total (see Table 1). Palpebral lobe crescentic, length (exsag.) 0.3 times cephalic length, narrow (width at midlength about 0.2 times length), with prominent palpebral rim and distinct palpebral rim furrow,  $\delta\delta$  0.8 times cephalic width and 1.35 times glabellar width. Palpebral furrow moderately impressed, shallowing opposite palpebral midlength, continuous with deep postocular furrow. Selera not raised. Anterior half of eye extending to librigenal border furrow, librigenal field poorly defined as a small depressed triangular area bounded by postero-lateral margin of eye, lateral border furrow and facial suture. Lateral border narrow and concave anteriorly, markedly widening posterior to midlength of eye, with shallow epiborder furrow extending to the point where the facial suture crosses the lateral margin. Cephalic doublure with sagittal length about 0.3 times cephalic length. Hypostomal suture transverse, with moderate median sag in anterior view.

Thoracic axial rings with strongly defined, quadrate, flat lateral nodes.

Pygidium lenticular in outline, with length about 0.5 times width, weakly convex. Axis raised, width 0.27 times pygidial width, moderately tapering, sides converging posteriorly at about 22°, reaching to 0.95 pygidial length, triangular terminal piece. First axial ring with well defined pseudo-articulating half-ring impressed into posterior margin, poorly defined on second and third rings, indistinct posteriorly. Interpleural furrows shallow but distinct. Pleural furrows deep and wide, shallowing abruptly adjacent to margin, lateral

border furrow and border poorly defined. Axial rings with coarse granulation. Pygidial doublure narrow, steeply inclined laterally, sub-vertical posteriorly, strongly convex in section.

Glabellar tuberculation comprising small, sparsely to densely distributed tubercles interspersed with dense ornament of granules, granulation coarser anteriorly, tubercles larger posteriorly. Palpebral area and postocular genae with subdued tuberculation. Fine granulation on remainder of exoskeleton.

*Remarks.* McCoy's (1876) description of '*Phacops (Portlockia) fecundus* Barrande, 1846' from Coldstream is based predominantly on specimens of *Lochkovella longisulcata*, and he listed a number of characters that are in accord with its assignment to *Lochkovella* including the long postocular genal length, the weak glabellar tuberculation, the granular surface ornament and the definition of the pygidial pleural and interpleural furrows. Etheridge & Mitchell (1896) referred McCoy's Coldstream specimens together with specimens from Loyola to their new species *Phacops sweeti*. However, Gill (1938) considered that the high lens counts of the Loyola specimens (22 rows, up to 12 lenses per row) distinguished them from the Coldstream specimens. Gill (1951) considered the latter represented one and possibly two new species, conclusions confirmed by their subsequent assignment to *Nephranomma debrae* Sandford, 2003 and *L. longisulcata*. Gill pre-empted the assignment of McCoy's specimens to *Lochkovella* in noting the morphology was intermediate between *Reedops* and *Phacops*, and close to *R. deckeri*.

*Lochkovella longisulcata* is closest to *L. misera*. These species differ from the *deckeri* group in exhibiting a distinct contrast in the grade of cephalic and post-cephalic ornament, a contrast stronger in *L. longisulcata*. In this respect these species are closest to *Ananaspis*. *Lochkovella longisulcata* further differs from the type species in having a slightly more broadly rounded glabellar anterior margin, sinusoidal rather than straight axial furrows; a larger eye (17-21, rarely 23-25 files of up to 7-10 lenses per file, see Table 1, cf. 13-14 files of up to 6 lenses per file in *L. misera*) that is more forwardly placed (anterior margin of eye opposite 0.7 rather than 0.65 cephalic length); glabellar tubercles that are slightly bigger and extend onto the genal areas, and finer interspersed granulation; and shallower pleural furrows posteriorly.

Variation within the populations assigned to *Lochkovella longisulcata* is considerable. Glabellar tuberculation ranges in density from sparse to dense and in size from small tubercles to coarse granules.

Tubercles on the smallest specimens are most prominent, as might be expected. More difficult to explain is the distinctly subdued ornament on specimens of both *L. longisulcata* and *Nephranomna debrae* in sandstone at PL1804 compared to specimens in siltstone at other localities; the differences appear to be real and cannot be attributed to preservation in a sandier matrix. Variation in glabellar ornament occurs between individuals from the same locality, but variations in eye size and lens arrangement appear to occur between populations from different localities. Specimens from the Tyers-Coopers Creek area have slightly shorter eyes/longer postocular genae than those from the Lilydale sequence, whereas those from the PL6751 (Coldstream) have somewhat longer eyes/shorter postocular genae than those from other localities. As there are no other consistent differences in degree of tuberculation, eye lenticulation or pygidial segmentation that further distinguish the various populations of *L. longisulcata*, they are considered to reflect natural intraspecific variation.

*Lochkovella longisulcata* occurs with *Nephranomna debrae* at several localities between the 1 750 m and 2 400 m horizons of the Humevale Siltstone. The two species are similar in overall appearance, but can always be distinguished by the shorter postocular genal length and larger eye in *N. debrae*. In addition, in *N. debrae* the glabellar tubercles are generally coarser; its eyes have higher lens counts (160-183 lenses in 10-11 files) and are placed more or less in exsagittal orientation; its cephalic doublure is more coarsely ornamented; and its pygidium is less deeply furrowed and only has five pleural furrows.

Four cephalons erroneously documented from the Late Wenlock-Early Ludlow Yan Yean Formation and previously described as *Ananaspis* sp. 1 (Sandford 1996) belong to *L. longisulcata*. The lithology and preservation of the specimens most closely matches that of the type locality PL1820, (G20, 'Ruddocks Quarry') from where they were probably collected.

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